funds are also put in place at the start of, and throughout, mining to pay for eventual closure and remediation. Should such practices continue, the global impacts of mine waste remobilization could be reduced in the future. Nevertheless, the amounts of mine wastes are still rising substantially, and it is now time to make a concerted global effort to predict and mitigate the potentially negative impacts of their remobilization.

Consolidated databases and inventories for mine waste sites have been created for some countries, such as Ireland (*13*). Such efforts need to be extended to the whole world to determine the impacts of global mining on biogeochemical cycles and on human and ecosystem health. Information is required on the locations, sizes, geochemistry, mineralogy, type of mining and processing, and other factors that will enable the global-scale sources, sinks, pathways, and fluxes of mine wastes to be quantified and their hazards identified. Such databases and research can be developed using existing information from academic studies, mining companies, and governmental surveys. However, ultimately they require the sponsorship and participation of funding agencies, governments and nongovernmental organizations, and international bodies such as the United Nations Environment Programme (UNEP), the World Business Council for Sustainable Development (WBCSD), and the Global Environment Facility to help with funding, data acquisition, implementing solutions, and raising global awareness of mine waste impacts and their remediation. ■

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Mycorrhizal associates. Trees allocate carbon to ectomycorrhizal fungi such as *Amanita muscaria*.

PHOTO: MARCEL VAN DER HEIJDEN

ECOLOGY

Underground networking

Fungal networks transfer carbon between forest trees

By **Marcel G. A. van der Heijden**[1,2,3]

Almost all land plants, including most trees, shrubs, and herbs, form symbiotic associations with mycorrhizal fungi (*1*). These soil fungi acquire nutrients that they transfer to their plant hosts in exchange for carbon (see the photo). Plants in natural vegetation can acquire up to 80% of nitrogen and phosphorus from their mycorrhizal associates (*2*). Individual mycorrhizal fungi can simultaneously colonize many plant hosts of the same species or different species. As a result, plants in natural communities are interconnected by mycorrhizal networks. Earlier studies with small tree seedlings revealed that carbon is transferred from one plant to another through these under-

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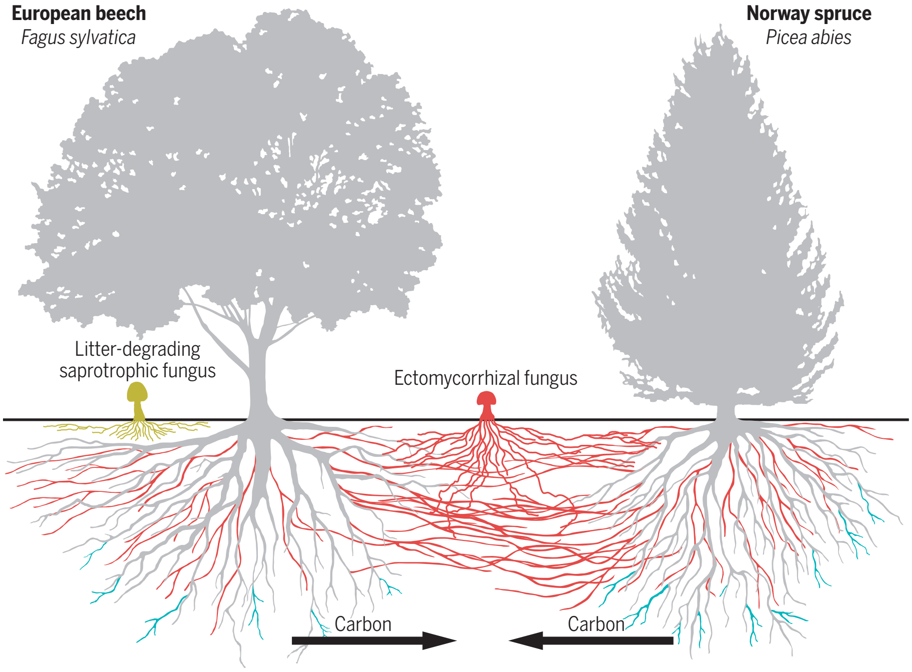
ground mycorrhizal pipelines (*3*). On page 342 of this issue, Klein *et al*. (*4*) show that interplant carbon transfer is not confined to tree seedlings.

The authors report forest-scale evidence for substantial tree-to-tree carbon transfer. Their results, obtained from 40-m-tall trees in a mixed forest in Switzerland, show that the equivalent of 280 kg carbon per hectare is transferred yearly between tree roots of different tree species. This is equivalent to 4% of the forest's net carbon uptake (also called its net primary productivity). Furthermore, the results indicate that under-

found depleted carbon in ectomycorrhizal fungal fruiting bodies near the labeled Norway spruce trees but not in the nonmycorrhizal saprotrophic fungi, nor in herbs that associated with a different type of mycorrhizal fungi (called arbuscular mycorrhizal fungi). These latter measurements acted as controls and provide evidence that ectomycorrhizal fungi act as carbon conducts.

The total amount of carbon that trees allocate to mycorrhizal fungi can be substantial; Wallander *et al*. have published estimates of 700 to 900 kg per hectare of forest (*6*). A proportion of this (~150 kg per



Underground networks. Forest trees are interconnected through extensive mycorrhizal fungal networks that can interlink different tree species. Carbon can move from one three to another through these hyphal networks.

ground mycorrhizal networks connecting the different tree species are, most likely, responsible for this carbon transfer.

Klein *et al*. use a highly sophisticated system to study carbon cycling in forests. Over a 5-year period, they labeled 40-m-tall Norway spruce trees with isotopically depleted CO_2, using a tall canopy crane and many porous tubes that released the labeled CO_2 near the branches of the trees (*5*). They then measured the carbon isotope signature in fine roots of neighboring unlabeled trees belonging to different taxa and also in unlabeled control trees that were not near labeled trees. The authors also measured the carbon signature in fruiting bodies (mushrooms) of mycorrhizal fungi that associate with the trees (called ectomycorrhizal fungi) and in fruiting bodies of litter-degrading saprotrophic fungi that do not form mycorrhizal associations. They

hectare) can be found in mycorrhizal root tips. Part of the carbon found in neighboring tree roots by Klein *et al*. may have remained in the fungal tissue of mycorrhizal structures (the fungal mantle surrounding tree roots and the fungal structures inside the roots) and was not transferred to the tree tissue (*7*). However, a substantial fraction of carbon was also acquired by the neighboring trees, as evidenced by enhanced isotope signal in the stems. This carbon may either have come directly from mycorrhizal fungi or some of it was acquired from the surrounding soil, e.g., through recapture of carbon from root exudates or root remains (*8*).

Overall, the results imply that large mature forest trees jointly maintain a common mycorrhizal network and that carbon can move freely from one tree to another tree through these belowground fungal highways (see the figure). These underground networks can be highly complex because each individual tree and fungus has its own network and can associate with different partners.

The results reported by Klein *et al*. also have implications for key questions in mycorrhizal research: Why is this symbiosis so widespread and why has it evolved so successfully? The observation that 4% of net primary productivity is transferred to neighboring trees suggests that carbon is a nonlimiting resource, and not growth-limiting for these large trees (*9*). Thus, carbon allocation and loss to mycorrhizal fungi does not necessarily impair plant fitness. The exchange of "nonlimiting" carbon for nutrients may be one of the key factors responsible for the evolutionary stability of the mycorrhizal symbiosis (*10*).

Klein *et al*. (*4*) measured 17 trees, 5 of which were the labeled trees that grew close to each other and were not randomly dispersed. As a result, replication is low. Further work in different forest ecosystems is needed to confirm the findings and their general validity. An interesting further question is which fraction of the carbon transferred between trees actually leaves the fungal tissue and is transferred to the tree.

An increasing number of studies show that belowground ecosystems are highly complex and diverse (*11*, *12*). Klein *et al*.'s study adds a new dimension to this, revealing that substantial amounts of carbon can move from one tree root system to another. Further work now needs to investigate whether trees benefit from this resource sharing and whether being interconnected through such mycorrhizal fungal networks enhances plant fitness and forest stability over evolutionary time. ■

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